



Numerical modelling and graph theory tools to study ecological connectivity in the Great Barrier Reef



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ABSTRACT

The process of coral larval dispersal is important for coral reef ecosystems, but remains poorly understood and hard to gauge. Better knowledge of inter-reef connectivity patterns would be useful in enabling better management of coral reef waters however. By employing a spatially explicit numerical modelling approach, we simulate larval dispersal through the central section of the Great Barrier Reef (GBR), comprising over 1000 reefs, and identify spatial patterns in the inter-reef connectivity network using a community detection method from network science. This paper presents the modelling approach used and discusses the significance of the results.

Inter-reef connectivity networks were estimated for 4 different coral species, and significant differences between them were found. We show how we can partition reefs into clusters, or “communities”, that are sparsely connected with each other, and therefore identify important barriers to larval dispersal. By fine-tuning a resolution parameter in the community detection method, we can find dispersal barriers of varying strength. Finally, we show that the average connectivity length scale varies significantly across the different reef communities, and suggest that this may have repercussions for the optimal placement of marine protected areas (MPAs) to maximise connectivity with surrounding reefs.

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1. Introduction

For most types of coastal marine species, the process of larvae dispersing through the ocean prior to reaching adulthood – known as the pelagic larval phase – is vital in enabling population exchange between geographically separated sub-populations (Cowen and Sponaugle, 2009; Cowen et al., 2006). In coral reef ecosystems the pelagic larval phase takes on an added importance as marine life is predominantly concentrated onto reefs of varying size separated by open sea. Many species of reef fish never leave their home reef as adults (Jones et al., 2009), whilst coral is physically fixed to the reef surface and is thus unable to travel between reefs. It is therefore only during the pelagic larval phase that these species can spread to new reefs, repopulate damaged

reef populations and maintain a healthy gene pool by exchanging larvae between separate sub-populations (Buston et al., 2012). Understanding how larvae disperse, where they can disperse to, and how resilient this process is to environmental change is essential to understanding the dynamics – and resilience – of coral reef ecosystems. Conservation strategies for coral reefs often involve the designation of Marine Protected Areas (MPAs) in which local anthropogenic interference is limited. In order for reefs in MPA networks to be effective in replenishing coral and reef fish populations in neighbouring reefs, the size and spacing of MPAs should account for the dispersal potential of marine species present in the region (Largier, 2003; Munday et al., 2009; Olds et al., 2012), which is not currently the case for most major coral reef ecosystems (Jones et al., 2009; Almany et al., 2009). Whilst some recent studies have proposed MPA designs which incorporate connectivity estimates to improve conservation performance, e.g. Mumby et al. (2011), Guizien et al. (2012), a major stumbling block so far has been a lack of location-specific knowledge of larval dispersion and

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connectivity patterns (Drew and Barber, 2012). Spatially explicit modelling studies such as the one presented in this article aim to fill this knowledge gap.

Larval dispersal remains very difficult to directly observe or measure, due to the small size of the larvae, the vastness of the ocean, and the fact that dispersion can occur over time-scales of days to weeks (Drew and Barber, 2012). Genetic tools can be used to measure the level of genetic connectivity between two given sub-populations, however these tools, whilst useful in quantifying present-day and historical connectivity, are by their nature unable to explain the processes driving the dispersion of larvae or to predict future trends (Palumbi, 2003), and are unable to provide spatially continuous detailed information over large regions. Numerical modelling tools can be used to fill this knowledge gap, both by providing large-scale estimates of present-day larval dispersion and connectivity patterns, and by showing how a change in physical or biological factors driving the dispersion process could alter inter-reef connectivity patterns (Werner et al., 2007).

The transport of larvae between separate reefs can be described in terms of “ecological” (or demographic) connectivity, which concerns the movement of individual larvae, or in terms of “genetic” connectivity, which concerns the exchange of genetic information. Ecological connectivity occurs over the time- and space-scales over which most larvae disperse (typically days to weeks and 0.1–100 km for coral) and is of primary interest for fisheries, reef management and MPA planning. Genetic connectivity on the other hand is a more complex process which plays out over many generations, with time- and space-scales spanning a greater range than ecological connectivity. For instance, the migration of just a few individuals per generation between two sub-populations can be enough to prevent genetic differences from developing, and can therefore represent a genetically significant level of connectivity (Cowen and Sponaugle, 2009; Leis et al., 2011), despite being ecologically insignificant. It is not a straightforward exercise to compare observed genetic connectivity with ecological connectivity predicted using large-scale numerical models as these models typically do not have enough precision to estimate transport down to ecologically insignificant (but still genetically significant) numbers of larvae, over time periods in the order of years.

In this paper we present a modelling approach to simulate larval dispersal down to reef-scale spatial resolution, and use this to study ecological connectivity in the region covering the central section of the Great Barrier Reef (GBR) in Australia, which includes roughly 1000 reefs. The GBR is a region with a particularly complex bathymetry and a correspondingly complex water circulation (Wolanski, 1994). Small-scale circulation at the reef-scale has been shown to interact significantly with large-scale circulation, for instance through the ‘sticky water’ effect (Wolanski and Spagnol, 2000; Wolanski et al., 2003; Andutta et al., 2012). In order to capture all major scales of motion, it is therefore necessary to resolve currents down to the reef scale: 100 m to 1 km. Present-day models of circulation in the GBR and other reef areas tend to have a horizontal resolution of 1–2 km however (e.g. Luick et al., 2007; Paris et al., 2007), too large to explicitly resolve flow at the lower range of larval dispersion length-scales, or even to capture many significant flow features in the reef-dense GBR. The use of nested structured grids is unfeasible in the GBR as the areas requiring enhanced resolution would be too numerous. In this study we instead use a finite element ocean model, SLIM,¹ to model water circulation in the GBR using an unstructured grid. This allows us to achieve reef-scale resolution around reefs at an acceptable computational

cost (Lambrechts et al., 2008). We then employ an Individual Based Model (IBM) to simulate the dispersion and settling of coral larvae through the domain.

Large-scale spatially-explicit simulations such as this can produce a huge amount of data, so a set of tools is needed to interpret this output if we are to draw useful conclusions. A number of mathematical tools have been developed to study properties of networks, including biological and ecological networks of geographically separate, connected populations (Proulx et al., 2005). The use of these tools in studies of coral connectivity has so far been limited however. Treml et al. (2008) showed how graph theory can be used to investigate dispersal pathways and identify ‘stepping-stone’ islands linking distant populations and, more recently, Kininmonth et al. used a graph theoretical approach to explore the robustness and scale (Kininmonth et al., 2010b) of a reef network, as well as spatial clustering of connections (Kininmonth et al., 2010a). Nilsson Jacobi et al. (2012) used community detection tools to identify sub-populations in a network of marine habitats for generic sessile invertebrates in the Baltic Sea, and to infer the presence of dispersal barriers. They also investigated how many clusters contained MPAs, and concluded that MPAs were poorly distributed amongst the clusters.

In the present study we explore the use of a graph theoretical approach to identify spatial patterns in large-scale connectivity of coral larvae. We use a community detection method to identify clusters of reefs which are ecologically isolated from each other, and we partition the central section of the GBR into such clusters, known as “reef communities”. Each reef community can be seen as a self-contained ecological sub-region, with little or no larvae exchanged with reefs in other communities. We establish maps delimiting separate reef communities in the GBR for 4 different species of coral, and find that significant inter-species differences exist in the size and shapes of the communities. These differences can be explained by variations in the biological characteristics of each species, and in particular their pre-competence periods. We also explore the differences in connectivity length scales across the different communities, and compare these to average MPA spacing. Such findings can potentially be used to inform the placement and spacing of MPAs to better take into account the different connectivity potential of larvae in each ecological sub-region.

This study has some parallels with Nilsson Jacobi et al. (2012), in which a similar graph theoretical approach to identify communities of generic sessile invertebrates in the Baltic Sea. Some differences of implementation between the two approaches are discussed in Section 2.3.2. No study that we are aware of has used these tools to compare the connectivity patterns of different marine species however, or to investigate whether dispersal patterns vary significantly in different sub-populations and how community-specific dispersal distances compare with MPA spacing.

2. Methods

The numerical modelling approach presented in this paper can be broadly divided into three stages: (1) modelling the hydrodynamics of the region, (2) simulating the transport of larvae, and (3) interpreting the model output. Each stage is now discussed, and a flow-chart summarising this process is presented in Fig. 2.

2.1. Resolving the hydrodynamics

2.1.1. Oceanographic model

Given the highly multi-scale nature of the water circulation in the GBR (as discussed in Section 1), it is important to use an ocean model able to cope with a large range of length scales. We used the finite element, unstructured-grid ocean model SLIM, in its

¹ Second-generation Louvain-la-Neuve Ice-ocean Model; see www.climate.be/slim for more information.

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